A comparative study of the dispersal of 10 species of stream invertebrates

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SUMMARY

1. Apart from downstream dispersal through invertebrate drift, few quantitative data are available to model the dispersal of stream invertebrates, i.e. the outward spreading of animals from their point of origin or release. The present study provides comparative data for 10 species, using two independent methods: unmarked animals in six stream channels built over a stony stream and marked animals in the natural stream. Experiments were performed in April and June 1973 and 1974, with initial numbers of each species varying from 20 to 80 in the stream channels and 20 to 60 for marked animals.
2. Results were the same for marked invertebrates and those in the channels. Dispersal was not density-dependent; the number of dispersing animals was a constant proportion of the initial number for each species. The relationship between upstream or downstream dispersal distance and the number of animals travelling that distance was well described by an inverse power function for all species (exponential and log models were poorer fits). Results varied between species but were similar within species for the 4 months, and therefore were unaffected by variations in mean water velocity (range 0.04–0.35 m s^{-1}) or water temperature (range 6.7–8.9 °C in April, 12.1–14.8 °C in June).
3. Species were arranged in order, according to their dispersal abilities. Three carnivores (*Perlodes, Rhyacophila, Isoperla*) dispersed most rapidly (70–91% in 24 h, maximum distances 9.5–13.5 m per day), followed by two species (*Protonemura, Rhithrogena*) in which about half their initial numbers dispersed (50–51% in 24 h, 7.5–8 m per day), and four species (*Ecdyonurus, Hydropsyche, Gammarus, Baetis*) in which less than half dispersed (33–40% in 24 h, 5.5–7 m per day). Dispersal was predominantly upstream for all nine species. Few larvae (20%) of *Potamophylax* dispersed, with similar maximum upstream and downstream distances of 3.5 m per day. The mean time spent drifting downstream was known for seven species from previous studies, and correlated positively with their dispersal distances. Therefore, the species formed a continuum from rapid to very slow dispersers. These interspecific differences should be considered when evaluating the role of dispersal in the maintenance of genetic diversity in stream invertebrates, and in their ability to colonise or re-colonise habitats.

Keywords: Ephemeroptera, *Gammarus*, invertebrate drift, Plecoptera, Trichoptera

Introduction

Dispersal is the outward spreading of organisms or propagules from their point of origin or release

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(Lincoln, Boxshall & Clark, 1998), and is essential for the maintenance of gene flow and genetic diversity, and also for colonisation and re-colonisation of habitat (Clobert *et al.*, 2001; Bullock, Kenward & Hails, 2002). Streams and rivers are ideal sites for dispersal studies because they have good spatial definition with well defined interfaces between air and water, and aquatic and terrestrial habitats. Previous studies have

focussed chiefly on 'invertebrate drift' which describes the downstream dispersal in the water column of benthic invertebrates that usually live on or amongst the substratum of the stream bed. Other movements occur vertically, transversely, upstream and downstream within or on the substratum of the stream bed (Allan, 1995; Palmer, Allan & Butman, 1996; Rader, 1997; Kopp, Jeschke & Gabriel, 2001). The challenge of quantifying and understanding the mechanisms of dispersal for stream invertebrates is now widely acknowledged and is being actively pursued, both in theoretical models and in models based on field experiments (e.g. Anholt, 1995; Lancaster, Hildrew & Gjerlov, 1996; McNair, Newbold & Hart, 1997; Fonseca, 1999; Bond, Perry & Downes, 2000; McNair, 2000; Kopp *et al.*, 2001; Elliott, 2002a–c).

Early studies of invertebrate drift showed that its impact on population density could not be assessed until more was known about the distances travelled by the drifting invertebrates. Several workers used an experimental approach to develop models, usually based on real data, to predict the distances travelled and time spent in the drift so that taxa could be grouped according to their settlement ability (references in Elliott, 2002a). There is no equivalent work on dispersal in other directions. In his review of upstream movements, Söderström (1987) included a section on the distance travelled, but cited only Elliott (1971a). However, some earlier estimates not mentioned in this review showed that upstream dispersal distances were either close to zero (Bishop & Bishop, 1968; Brusven, 1970; Neves, 1979; Bird & Hynes, 1981) or large (Neave, 1930; Ball, Wojtalik & Hooper, 1963; Meijering, 1972; Hayden & Clifford, 1974; Erman, 1986). More recent work also shows that upstream dispersal is negligible (Hancock & Hughes, 1999) or extensive (Freilich, 1991; Rawer-Jost *et al.*, 1999). Dispersal models were not fitted in any of these studies apart from that by Freilich (1991) who concluded that movements of a stonefly, *Pteronarcys californica* (Newport), differed significantly from random walk models, and were strongly directional to 'zones of attraction'.

Central to the theory of dispersal in stream invertebrates is the role of density-dependent processes. Waters (1972) found that, with few exceptions, there was no direct relationship between drift rate and benthic density. Several field and experimental studies supported this lack of density dependence (Reisen

& Prins, 1972; Hildebrand, 1974; Madsen, 1976; Bohle, 1978; Corkum, 1978; Ploskey & Brown, 1980; Ciborowski, 1983; Turner & Williams, 2000; Elliott, 2002b,c). Others have supported a relationship (Gyselman, 1980; Turner & Williams, 2000), or have shown that downstream dispersal can be density-dependent or density-independent, depending upon the water velocity (Walton, 1980), type of substratum (Walton, Reice & Andrews, 1977), or the season and period in the life cycle (Kerans, Chesson & Stein, 2000). Only one experimental study has examined both upstream and downstream dispersal in relation to benthic density. Thus, Humphries (2002) found that dispersal of a mayfly species, *Baetis rhodani* (Pictet), in either direction was proportional to benthic density and therefore density-independent. No information was provided on distances travelled because of the short length of the channel.

Apart from data on downstream dispersal through drifting, there is a paucity of quantitative data that can be used to model the dispersal distances of stream invertebrates and examine the role of density-dependence. The present study provides comparative data for 10 species that are found frequently in stony streams. The species were chosen so that they came from different taxonomic and functional feeding groups. The textbook of Southwood (1966) was probably the first to recommend that ecological parameters should be estimated by more than one method. This was done in the present study. Dispersal distances were measured for unmarked animals in six stream channels built above a stream, and for marked animals in the natural stream.

Materials and methods

Study site and species

The experiments were performed in Wilfin Beck, a small stream (length 4 km) in the English Lake District. The stream was described in detail by Elliott (1973). The experimental site (latitude 54°20′N, longitude 3°2′W) was a 60-m stretch in a steep section (fall about 4%) near the mouth of the stream, and was a mixture of riffles and runs with no deep pools. The substratum was large stones (diameter up to 0.3 m) over smaller stones and gravel, with sparse clumps of bryophytes on the larger stones and exposed bedrock. Experiments were performed in April and June 1973

and 1974. Modal depth ranged from 0.10 m (1974) to 0.17 m (1973) in April, and was 0.16 m in June (1973, 1974). Modal width ranged from 3.20 (1974) to 3.7 m (1973) in April, and was 3.5 m in June (1973, 1974). Fifty measurements of water velocity 3 cm above the surface of the substratum were taken within the experimental site, using a miniature current meter. Values were very low in April 1974 with a mean of 0.04 m s^{-1} (range 0.02–0.06 m s^{-1}) and highest in April 1973 with a mean of 0.35 m s^{-1} (range 0.28–0.46 m s^{-1}). Values were closer in June with means of 0.14 m s^{-1} (range 0.10–0.20 m s^{-1}) in 1973 and 0.17 m s^{-1} (range 0.12–0.26 m s^{-1}) in 1974. A maximum and minimum thermometer was read and reset underwater daily during the experiments. Values were similar in the same month, with April ranges of 6.7–8.1 °C in 1973 and 7.5–8.9 °C in 1974, and June ranges of 12.7–14.8 °C in 1973 and 12.1–13.8 °C in 1974. Oxygen concentration was measured four times a day, using a Mackereth (1964) meter, and was always over 85% saturation.

Elliott & Bagenal (1972) showed that electro-fishing caused a marked increase in the number of invertebrates drifting downstream but did not greatly disturb the stream bed. Therefore, a pulsed DC shocker (Moore, 1968) was used to collect invertebrates from the substratum immediately downstream from the experimental site. The circular anode of the shocker was replaced by a stainless steel rod which was inserted to a depth of about 10 cm in the substratum. The drifting invertebrates were caught in three pond nets, each having a rectangular mouth (width 250 mm, height 220 mm) and a mesh aperture of 950 μm. As only invertebrates greater than half-size were large enough to mark, they were used in all experiments to ensure comparability. Half-size was half the mean length of the final instar, with the length measured from the front of the head to the tip of the abdomen to the nearest millimetre.

The following 10 species were collected in sufficient numbers for the experiments (half sizes are given in parentheses): three species of Plecoptera, the carnivores *Perlodes microcephalus* (Pictet) (11 mm) and *Isoperla grammatica* (Poda) (7 mm), and the herbivore *Protonemura meyeri* (Pictet) (5 mm); three species of herbivorous Ephemeroptera, *Ecdyonurus venosus* (Fabricius) (7 mm), *Rhithrogena semicolorata* (Curtis) (6 mm) and *B. rhodani* (6 mm); three species of Trichoptera, the carnivore *Rhyacophila dorsalis* (Curtis)

(8 mm), the net-spinning filter-feeder *Hydropsyche siltalai* Döhler (7 mm) and the case-building shredder *Potamophylax cingulatus* (Stephens) (8 mm); and the omnivorous freshwater shrimp *Gammarus pulex* L. (6 mm). *Potamophylax cingulatus* was not induced to drift and had to be collected by hand-searching under large stones. As there was only one species in each genus, generic names only are used in the results.

Experimental stream channels

Channels were made from plastic guttering fastened to metal supports so that they were just above the water surface for most of their length. There were six parallel channels, each with a length of 21 m and a width of 0.1 m at the surface of the substratum which consisted of smaller stones (diameter 1–5 cm) obtained from the stream and cleaned to remove animals but not algae. The upstream end of each channel was below the water surface in a small waterfall and water velocity was regulated by a sluice gate so that it was the same for the six channels in each monthly set of experiments. As the water velocity depended on stream flow, it varied between months, being lowest at 0.04 m s^{-1} in April 1974 and highest at 0.35 m s^{-1} in April 1973, with intermediate values in June of 0.12 m s^{-1} in 1973 and 0.15 m s^{-1} in 1974. These values were the means of readings taken just above the substratum every metre along each channel with a miniature current meter. Water depth above the substratum varied from 0.05 m at the lowest velocity to 0.07 m at the highest. Nets at the two ends of each channel prevented the entry of invertebrates.

Invertebrates were introduced at mid-day (12 : 00 h) into a 1-m long section (area 0.1 m^2) at the centre of each channel, and were retained for 24 h by screens (mesh aperture 950 μm) at the upstream and downstream ends of the section. This time allowed the invertebrates to disperse and become accustomed to the conditions within the section. Initially, invertebrates were absent from the rest of the channel. The initial number of animals introduced into the central section was one of six values (20, 30, 40, 50, 60, 80 per 0.1 m^2) which were allocated at random between the six channels. The screens were removed on the next mid-day so that the invertebrates were free to move upstream or downstream for a maximum distance of 10 m in either direction. The nets at the two ends of the channel caught any animals

attaining the maximum distance. After 24 h, the screens were replaced in the central section and additional screens (mesh aperture 950 μm) were inserted at 0.5 m intervals along the channel. The substratum was removed from each 0.5 m section and the invertebrates counted. This procedure provided information on the net distances (to nearest 0.5 m) travelled upstream or downstream, and the number of animals travelling these distances in 24 h. Animals remaining in the central section were deemed to have travelled only 0.5 m, i.e. half the length of the section in either direction. All experiments with the same species were performed simultaneously in each month, and took 2 days. Replication at each initial number was not possible because of the limited number of stream channels. Experiments were repeated over 4 months (April, June 1973, 1974) with the six initial numbers in each month, to provide 24 data points at each distance for each species.

Marking experiments

Individuals of eight of the 10 species were marked by first blotting dry the dorsal surface of the thorax, then applying a spot of quick-drying cellulose paint (nail varnish). Paint was applied to the case of *Potamophylax*, rather than the thorax, whereas *Baetis* larvae were marked by placing them in a weak solution (0.5 ‰ isotonic saline) of methylene blue, neutral red or Janus green B for 12 h. Previous experiments have shown these marking techniques did not affect the invertebrates (Elliott, 1971b), a conclusion that was confirmed by the high recapture rate in the present experiments.

Marked animals of the same species were placed in a wooden box (floor dimensions 0.25 × 0.25 m with height of 0.08 m). The box bottom was a coarse mesh covered with nylon netting (mesh aperture 390 μm) to prevent escape or entry of invertebrates. The sliding top of the box was covered with the same netting. Before adding the animals, the box bottom was covered with small stones (diameter 2–4.5 cm) from the stream. To reduce the possibility of carnivores eating each other, their boxes were divided by perforated metal partitions into 25 compartments, each 0.05 × 0.05 m, and the animals were distributed in similar numbers in each compartment. This procedure did not appear to inhibit the dispersal of these larvae because none was left in the box after release.

The box containing a known number of marked invertebrates was then embedded in the stream bed so that the top was level with the substratum surface and any hydraulic effects were reduced to a minimum. Each box was closed for 24 h to allow the animals to adjust to the conditions in the box. The initial number of animals was one of three values for each species (20, 40, 60 per box) and a different colour of paint or dye was used for each initial number. Thirty boxes were placed in the stream so that the experiments for all species and initial numbers were performed simultaneously in each month. The boxes were arranged in a grid with three rows of 10 boxes across the stream, each box being allocated at random. The grid covered an area with a width of 2.5 m in the centre of the stream and an upstream-downstream distance of 0.75 m.

After they had been left in the stream for 24 h, the tops of all boxes were removed so that the animals were free to move upstream or downstream. After a further 24 h, the boxes were searched and then the electro-shocker was used to retrieve the dispersed invertebrates. Any marked animals found in the boxes or within 0.125 m of the boxes were deemed to have travelled 0.5 m, i.e. half the upstream-downstream length of the 1 m stretch containing the boxes. The stream was searched systematically by moving away from the boxes, first in a downstream direction and then upstream, both for a maximum distance of 20 m. When marked animals were caught, their distance from the stretch containing the boxes was measured to the nearest 0.5 m. Larvae of *Potamophylax* were not caught by electro-fishing and had to be collected by hand-searching under large stones. Information was thus obtained for the distances travelled upstream or downstream, and the number of marked animals travelling these distances in 24 h.

Data analysis

Standard linear regression analysis, residual analysis, and analysis of covariance (ANCOVA) were used. Several regression equations used to describe distributions of dispersal distances were compared by Taylor (1978) and Turchin (1998), who showed that equations using negative exponential functions or inverse power functions were used most frequently, the latter being less likely to underestimate the longer distance movements. Three of these equations were

tested in the present study; negative exponential, negative logarithmic and inverse power. Data on the distance travelled [L (m)] and the proportion of animals travelling that distance (%D) were linearly transformed before regression analysis, using either a semi-ln plot for the negative exponential (ln %D on L), a semi-ln plot for the negative logarithmic (%D on ln L), and a double-ln plot for the inverse power model (ln %D on ln L). Regressions were weighted according to the number of recaptures. For all analyses, the power model provided the lowest residual mean square and was therefore used to describe the results. The other two models provided too shallow a curve to fit the data.

Results

Experimental stream channels

All animals were retrieved for seven species. Losses for the other three species were probably the result of adult emergence because cast skins of the final larval instar were found in the downstream net. These losses were very small compared with the 280 animals used for each species in each month with a maximum of eight lost in a single trial. In all presentations of results, species were ranked from highest to lowest according to the proportion dispersing from the central section (Tables 1 and 2, Figs 1–5).

The relationship between the number (D) of animals dispersing from the central section and their initial number (N per 0.1 m^2) was linear for all species (Fig. 1) and well described by:

$$D = a + bN \tag{1}$$

where values of a and b varied between species (Table 1). All regressions were highly significant ($P < 0.001$) with high adjusted r^2 values (Table 1). Therefore, dispersal was not density-dependent. The number of dispersing animals was a constant proportion of the initial number for each species. Although the proportion of animals dispersing in 24 h was unaffected by initial number, mean values (mean %D with $n = 24$) varied considerably between species from 91% for *Perlodes* to only 20% for *Potamophylax* (Table 2). The monthly values for 4 months at each initial number were very similar within each species. ANCOVA revealed no significant differences ($P > 0.05$) between values for the 4 months, and residual analysis showed that the number dispersing was unaffected by variations in mean water velocity or water temperature.

The number of animals dispersing upstream (D_U) or downstream (D_D) was also related linearly to initial number. Therefore, the ratio of upstream to downstream dispersers (D_U/D_D) was not affected significantly by initial number (closed diamonds in Fig. 2). ANCOVA revealed no significant differences between values for the 4 months and residual analysis showed that the ratio was unaffected by variations in water velocity or temperature. The upstream–downstream ratio was close to equality for *Potamophylax* (Fig. 2; Table 2) For all other species, dispersal was predominantly upstream with a positive correlation between the dispersal ratio and the proportion of animals dispersing ($r = 0.99$ with $n = 10$).

Table 1 Stream channels: estimates of the constants a and b (both with 95% CL) for the linear equation 1 ($D = a + bN$), and for the power function (equation 2: %$D = aL^{-b}$) fitted separately to data for upstream and downstream moving animals, with adjusted coefficients of determination (r^2) and number of mean values used in each analysis (n)

	Equation 1				Equation 2: upstream moving				Equation 2: downstream moving			
	a	b	r^2	n	a	b	r^2	n	a	b	r^2	n
Perlodes	0.20 ± 1.49	0.90 ± 0.03	0.99	24	6.71 (6.46–6.97)	0.52 ± 0.02	0.99	19	6.68 (6.61–6.75)	0.51 ± 0.02	0.99	5
Rhyacophila	0.28 ± 1.40	0.80 ± 0.03	0.99	24	9.93 (9.70–10.17)	0.96 ± 0.02	0.99	19	9.97 (9.76–10.19)	0.98 ± 0.04	0.99	4
Isoperla	0.18 ± 1.55	0.70 ± 0.03	0.99	24	12.55 (11.63–13.54)	1.24 ± 0.05	0.99	19	12.23 (10.50–14.24)	1.29 ± 0.33	0.99	3
Protonemura	0.83 ± 1.53	0.49 ± 0.03	0.98	24	12.41 (10.95–14.06)	1.71 ± 0.09	0.99	16	12.76 (1.56–85.49)	1.83 ± 1.48	0.93	3
Rhithrogena	−0.15 ± 1.58	0.51 ± 0.03	0.98	24	12.33 (10.68–14.25)	1.70 ± 0.10	0.98	16	12.08 (2.28–63.87)	1.91 ± 2.59	0.96	3
Ecdyonurus	0.00 ± 1.39	0.40 ± 0.03	0.98	24	11.07 (8.83–13.88)	1.95 ± 0.17	0.98	14	11.34 (1.96–65.40)	2.24 ± 3.78	0.98	3
Hydropsyche	0.10 ± 1.18	0.40 ± 0.02	0.98	24	11.67 (9.89–13.77)	2.11 ± 0.13	0.99	13	11.70 (2.73–50.10)	2.27 ± 3.14	0.98	3
Gammarus	−0.10 ± 1.42	0.34 ± 0.03	0.96	24	10.99 (9.20–13.13)	2.40 ± 0.15	0.99	12	10.08 (1.81–56.15)	2.62 ± 3.71	0.98	3
Baetis	−0.55 ± 1.09	0.36 ± 0.02	0.98	24	10.70 (8.43–13.59)	2.38 ± 0.21	0.98	11	9.96 (1.78–55.71)	2.61 ± 3.71	0.98	3
Potamophylax	0.03 ± 0.83	0.20 ± 0.02	0.96	24	7.14 (5.01–10.19)	3.21 ± 0.43	0.98	7	7.28 (4.69–11.31)	3.10 ± 0.53	0.97	7

Table 2 Stream channels: mean values for the percentage of animals dispersing (mean %D), the ratio of number of animals moving upstream to those moving downstream (D_U/D_D), the median [Med. L (m)] and maximum [Max. L (m)] distances moved upstream and downstream (downstream values exclude animals caught in the net at 10 m), and the mean time (s) spent drifting downstream (values from Elliott, 2002a); 95% CL given for all values except Max. L (m)

	Mean %D	D_U/D_D	Med. L (m) up	Med. L (m) down	Max. L (m) up	Max. L (m) down	Drift time (s)
Perlodes	90.54 ± 1.52	3.13 ± 0.10	4.35 ± 0.16	1.50 ± 0.05	10+	3.0	–
Rhyacophila	80.33 ± 1.37	2.68 ± 0.09	3.06 ± 0.24	1.04 ± 0.06	10+	2.0	–
Isoperla	70.38 ± 1.32	2.59 ± 0.11	2.11 ± 0.15	0.92 ± 0.05	9.5	1.5	–
Protonemura	50.90 ± 1.43	1.98 ± 0.10	1.41 ± 0.07	0.97 ± 0.06	8.0	1.5	33 ± 0.3
Rhithrogena	50.20 ± 1.77	2.08 ± 0.07	1.38 ± 0.08	0.94 ± 0.06	8.0	1.5	33 ± 0.3
Ecdyonurus	40.20 ± 1.35	1.76 ± 0.08	1.05 ± 0.04	0.93 ± 0.07	7.0	1.5	17 ± 0.5
Hydropsyche	40.19 ± 1.16	1.66 ± 0.08	1.04 ± 0.05	0.88 ± 0.07	6.5	1.5	22 ± 0.9
Gammarus	33.76 ± 1.31	1.62 ± 0.08	0.93 ± 0.05	0.90 ± 0.07	6.0	1.5	9 ± 0.3
Baetis	33.06 ± 1.22	1.60 ± 0.08	0.95 ± 0.04	0.89 ± 0.05	5.5	1.5	9 ± 0.3
Potamophylax	20.08 ± 0.90	1.01 ± 0.09	0.92 ± 0.05	0.90 ± 0.05	3.5	3.5	1–4

The relationship between distance travelled [L (m)] and the proportion of animals travelling that distance (%D) was described by an inverse power function:

$$\%D = aL^{-b} \qquad (2a)$$

or

$$\ln \%D = \ln a - b \ln L \qquad (2b)$$

where values of a and b varied between species (Table 1). The mean of the 24 values at each distance (values for the six initial densities in each of 4 months) was estimated with high precision (note narrow 95% CL in Figs 3–5). Therefore, to avoid the problem of zero values in the regression analyses, only mean values were used. This procedure reduced the sample size and sometimes led to poor precision in the estimates of a and b, especially for downstream-moving animals. An alternative procedure would have been to add one to all values so that they were all used, but this would have led to a strong bias in the tail of the distribution. All regressions were highly significant ($P < 0.001$) with high adjusted r^2 values (Table 1).

As the proportion dispersing varied considerably between species, it was impossible to present all data on the same scales. Therefore, species were grouped according to their rates of dispersal (Figs 3–5). The first point is the proportion of animals dispersing only 0.5 m, i.e. the proportion of animals remaining in the central section. The three carnivores (*Perlodes*, *Rhyacophila*, *Isoperla*) dispersed most rapidly (70–91% in 24 h), predominantly in an upstream direction (Fig. 3). A few *Perlodes* and *Rhyacophila* were caught in the upstream net and these were the only species to

attain the maximum distance upstream. Two *Rhyacophila* and two *Isoperla* were caught in the downstream net and could have drifted downstream. About half the initial numbers of *Protonemura* and *Rhithrogena* dispersed with maximum distances of 8 m upstream and only 1.5 m downstream (Fig. 4a–d). About 40% of the initial numbers of *Ecdyonurus* and *Hydropsyche* dispersed with maximum distances of 6.5–7.0 m upstream and only 1.5 m downstream (Fig. 4e–h). None of these four species was taken in the upstream or downstream nets. About 33% of *Gammarus* and *Baetis* dispersed with maximum distances of 5.5–6.0 m upstream and only 1.5 m downstream (Fig. 5a–d). Seven *Gammarus* and seven *Baetis* were caught in the downstream net and were assumed to have drifted downstream. Only 20% of *Potamophylax* dispersed and maximum upstream and downstream distances were equal at 3.5 m (Fig. 5e,f).

Median dispersal distances were defined as the distance travelled by 50% of the animals dispersing in the same direction, excluding those animals remaining in the central section. Upstream median values ranged from 4.35 m for *Perlodes* to 0.92 m for *Potamophylax*, whilst downstream values ranged from 1.5 m for *Perlodes* to 0.90 m for *Potamophylax* (Table 2). For all species, there was a positive correlation between the median dispersal distance upstream or downstream and the proportion of animals dispersing ($r = 0.93$ and 0.75 for upstream and downstream values, respectively, with $n = 10$). The power b in equation 2 provided an inverse index of the rate of dispersal with low values indicating rapid dispersal
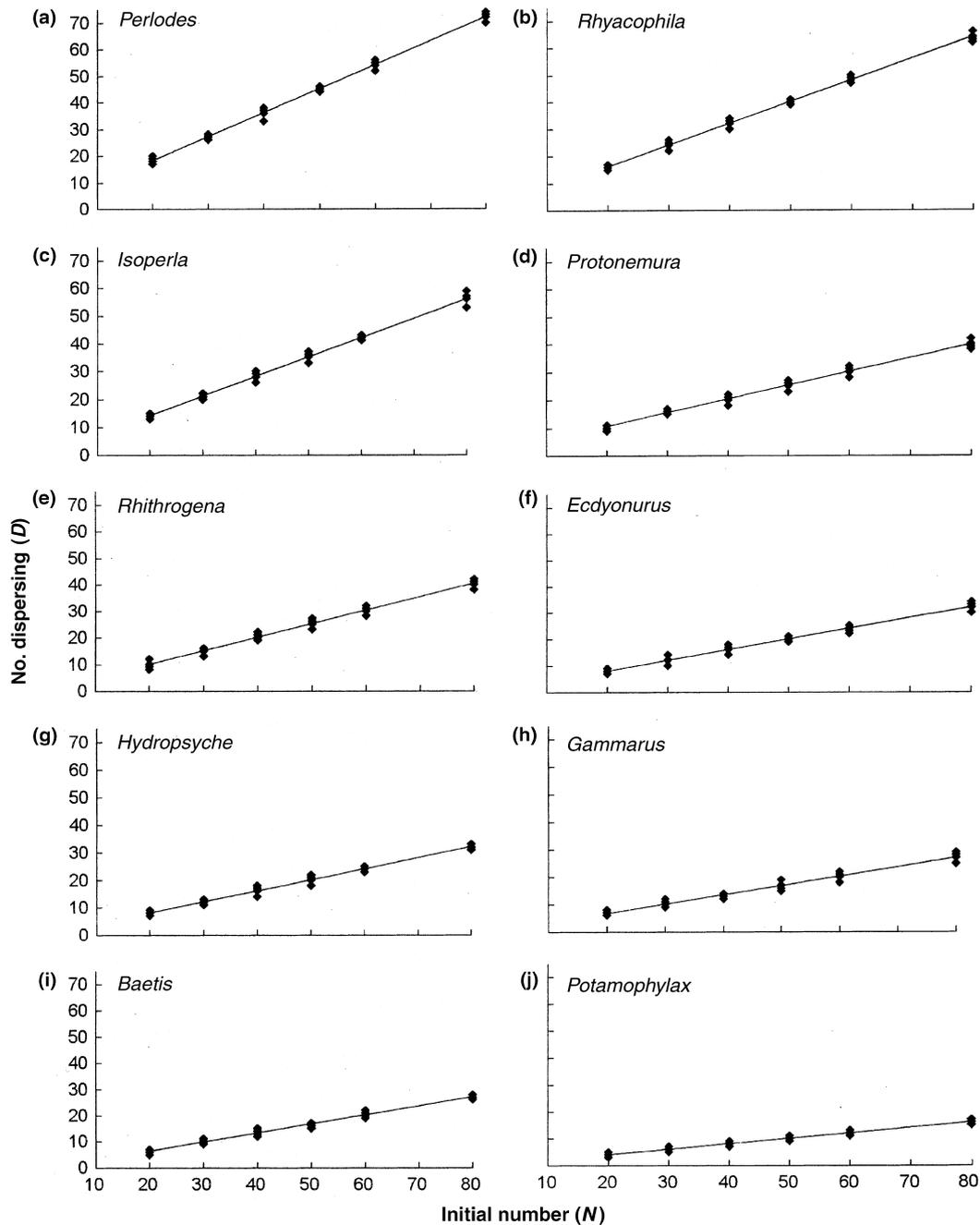
Fig. 1 Relationship between number (*D*) of animals dispersing and their initial number (*N* individuals per 0.1 m^2) for stream channels; regression lines given by equation 1 in Table 1. (a) *Perlodes microcephalus*, (b) *Rhyacophila dorsalis*, (c) *Isoperla grammatica*, (d) *Protonemura meyeri*, (e) *Rhithrogena semicolorata*, (f) *Ecdyonurus venosus*, (g) *Hydropsyche siltalai*, (h) *Gammarus pulex*, (i) *Baetis rhodani* and (j) *Potamophylax cingulatus* (note that there were four values for each *N* value but this is not always apparent because some values coincided).

and high values slow dispersal (Table 1). For each species, *b* values were not significantly different (*P* > 0.05) for upstream and downstream moving animals (Table 1). Therefore, dispersal rates were similar in either direction and the greater distances travelled upstream were probably because of the larger number of animals travelling in that direction for all species except *Potamophylax*.
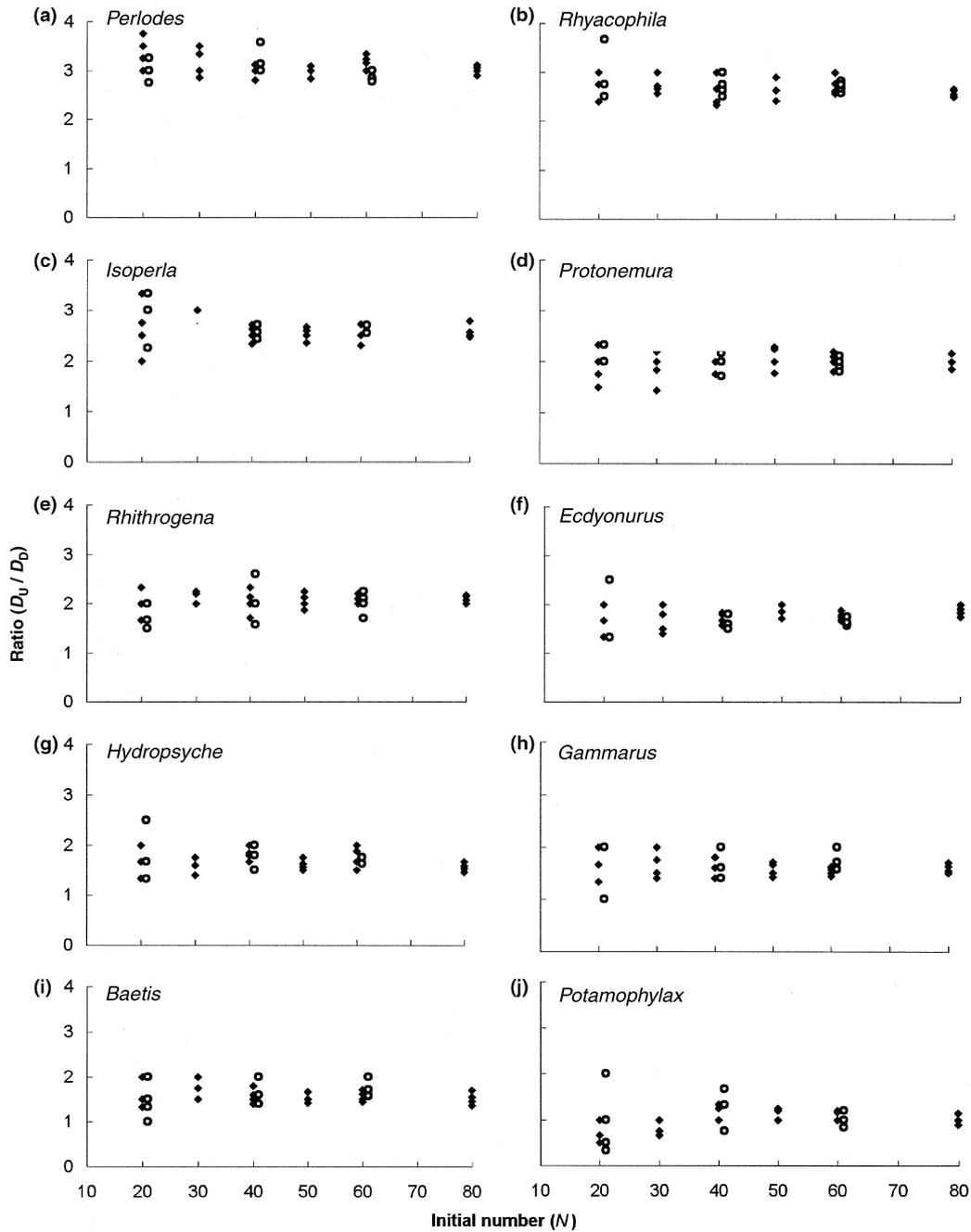
Fig. 2 Relationship between the ratio D_U/D_D and initial number (N) for stream channels (closed diamonds), and marking experiments (open circles). D_U = number dispersing upstream, D_D = number dispersing downstream; species names were the same as those given for (a) to (j) in Fig. 1. Values of N were 20, 30, 40, 50, 60 and 80 individuals per 0.1 m^2 in the stream channels, and 20, 40, and 60 individuals per box (area 0.0625 m^2) in the marking experiments (note that there were four values for each N value but this is not always apparent because some values coincided).

In summary, the relationship between upstream or downstream dispersal distance and the number of animals travelling that distance was well described by a negative power function for all species, and the relationship was similar within species but varied between species.
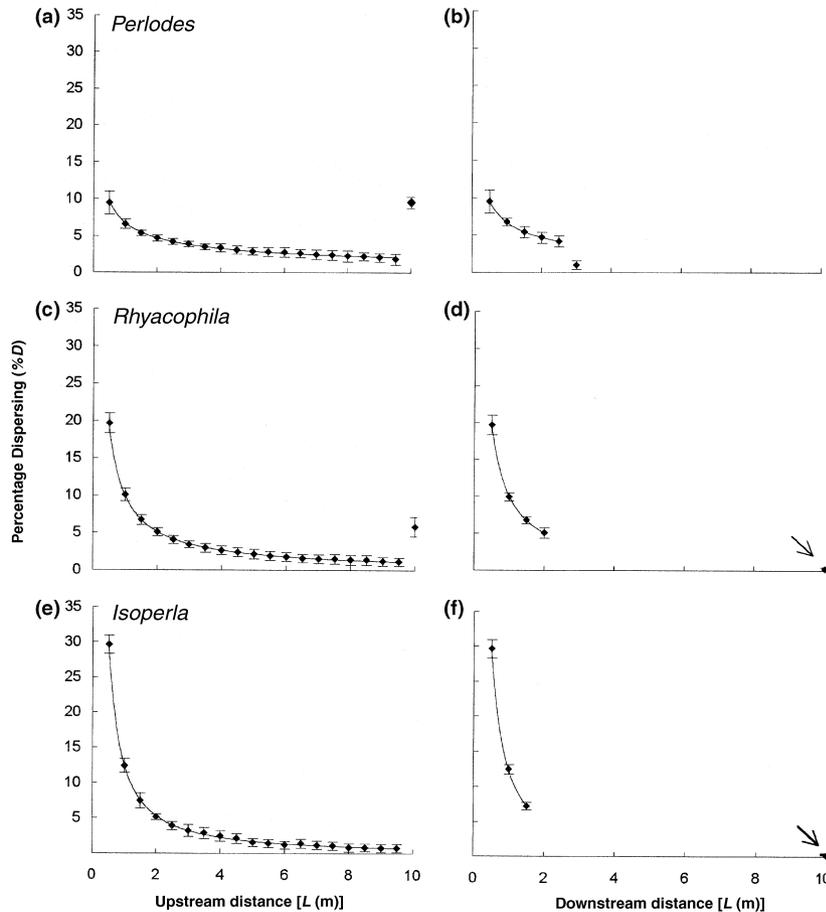
Fig. 3 Stream channels: relationship between the distance travelled [*L* (m)] upstream (left panels) or downstream (right panels) and the proportion of animals travelling that distance (%*D*); curves given by equation 2 in Table 1. (a and b) *Perlodes microcephalus,* (c and d) *Rhyacophila dorsalis* and (e and f) *Isoperla grammatica* [arrows in (d) and (f) indicate animals caught in the downstream net] (each point is the mean with 95% CL).

Marking experiments

All animals left the boxes, apart from a few *Potamophylax*, but some were found near the boxes and were recorded as travelling only 0.5 m. None of the marked animals was recaptured at distances greater than 13.5 m upstream and 14 m downstream. Some marked animals were never found. These losses varied between 5 and 15% of the initial number and were possibly because of adult emergence for some species, mortality within the stream, dispersal beyond the area searched, or simply failure to find the marked animals. Six empty marked cases of *Potamophylax* were recovered and recorded as losses.

Although there were only three values for the initial number (20, 40 and 60 per box), the relationship between the number dispersing (*D*) from the central section and their initial number (*N* per box) was linear for all species, and well described by equation 1. All regressions were significant ($P < 0.001$) with high adjusted r^2 values (Table 3). The number dispersing upstream (D_U) or downstream (D_D) was also linearly related to initial number. Therefore, the ratio D_U/D_D was not affected significantly ($P > 0.05$) by initial number (open circles in Fig. 2). For both this ratio and values of *D*, residual analysis indicated no significant effects ($P > 0.05$) because of variations in mean water velocity (range 0.04–0.35 m s^{-1}) or temperature (range 6.7–14.8 °C) for the four marking experiments in different months. Therefore, the marking experiments also showed that dispersal was not density dependent.

Mean values for the proportion dispersing (mean %D_1 with $n = 12$) varied between species (Table 4) and were lower than those obtained from the stream channels (Table 2). However, when the data were corrected for non-recaptures, mean values (mean %D_2 in Table 4) were similar to those from the channels. Dispersal ratios (D_U/D_D in Table 4; closed circles for
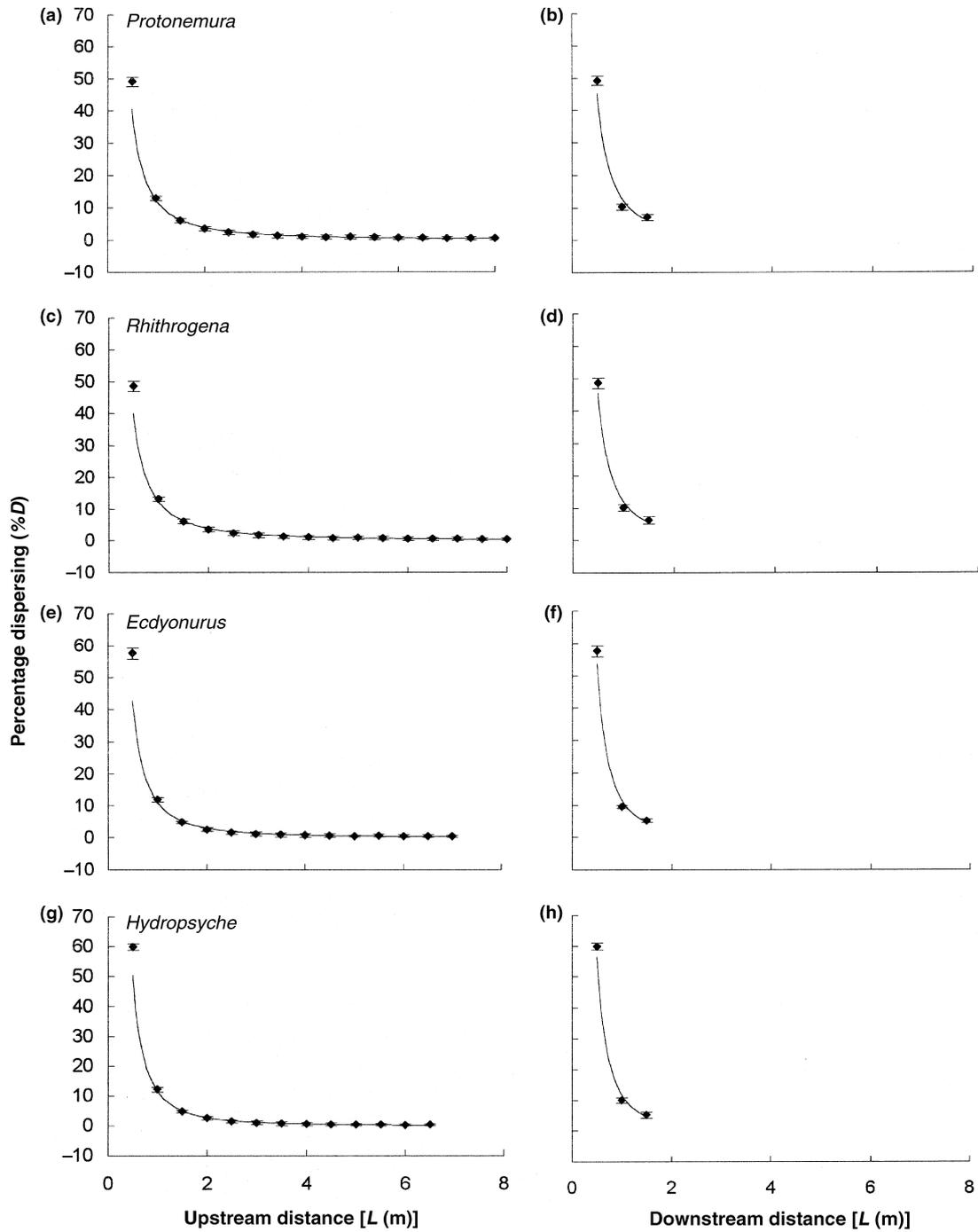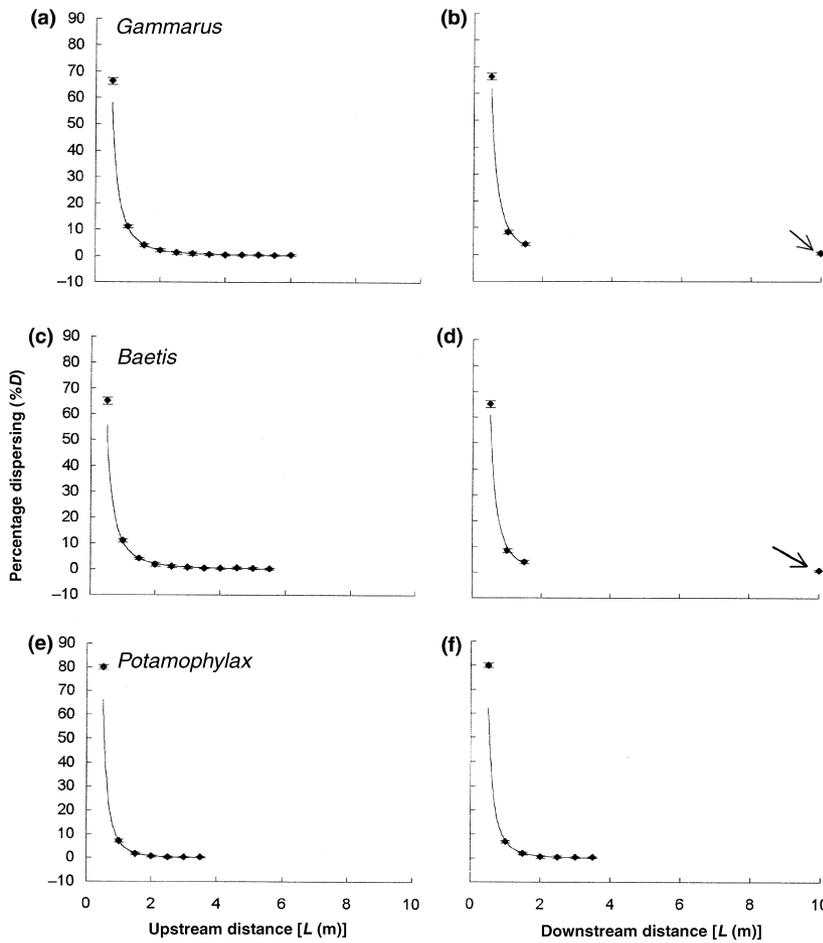
Fig. 4 Stream channels: relationship between the distance travelled [L (m)] upstream (left panels) or downstream (right panels) and the proportion of animals travelling that distance (%D); curves given by equation 2 in Table 1. (a and b) *Protonemura meyeri*, (c and d) *Rhithrogena semicolorata*, (e and f) *Ecdyonurus venosus* and (g and h) *Hydropsyche siltalai* (each point is the mean with 95% CL).

$N = 20$, 40 and 60 in Fig. 2) were also very similar to those from the channels, and were positively correlated with the proportion of animals dispersing ($r = 0.99$ with $n = 10$).

To avoid repetition of figures similar to Figs 3–5, the relationship between the distance travelled [L (m)] and the proportion of animals travelling that distance (%D) was illustrated for only four species

Fig. 5 Stream channels: relationship between the distance travelled [*L* (m)] upstream (left panels) or downstream (right panels) and the proportion of animals travelling that distance (%*D*); curves given by equation 2 in Table 1. (a and b) *Gammarus pulex*, (c and d) *Baetis rhodani* and (e and f) *Potamophylax cingulatus* [arrows in (b) and (d) indicate animals caught in the downstream net] (each point is the mean with 95% CL).

(Fig. 6). As the proportion dispersing varied considerably between these four species, the data for %*D* had to be presented on different scales. Regression equations were fitted to data for all ten species,

using equation 2, and the fitting procedure was the same as that used for data from the stream channels. All regressions were highly significant ($P < 0.001$) with high adjusted r^2 values (Table 3). Relationships

Table 3 Marking experiments: estimates of the constants *a* and *b* (both with 95% CL) for the linear equation 1 ($D = a + bN$), and for the power function (equation 2: $\%D = aL^{-b}$) fitted separately to the data for upstream and downstream moving animals, with adjusted coefficients of determination (r^2) and number of mean values used in each analysis (*n*)

	Equation 1				Equation 2: upstream moving				Equation 2: downstream moving			
	a	*b*	r^2	*n*	*a*	*b*	r^2	*n*	*a*	*b*	r^2	*n*
Perlodes	−0.42 ± 1.41	0.83 ± 0.03	0.99	12	6.60 (6.22–6.99)	0.55 ± 0.03	0.98	22	6.09 (5.84–6.34)	0.54 ± 0.06	0.99	5
Rhyacophila	−0.42 ± 1.57	0.73 ± 0.04	0.99	12	8.80 (8.48–9.13)	0.95 ± 0.02	0.99	26	9.00 (7.91–10.24)	0.97 ± 0.24	0.99	4
Isoperla	0.00 ± 1.44	0.63 ± 0.03	0.99	12	12.40 (9.21–16.68)	1.38 ± 0.19	0.93	19	10.72 (8.14–14.12)	1.31 ± 0.59	0.99	3
Protonemura	−0.17 ± 1.05	0.47 ± 0.02	0.99	12	12.38 (10.44–14.69)	1.77 ± 0.13	0.98	13	11.46 (1.54–85.40)	1.83 ± 4.33	0.93	3
Rhithrogena	0.00 ± 1.08	0.45 ± 0.03	0.99	12	12.15 (8.80–16.78)	1.79 ± 0.22	0.96	14	11.54 (1.02–128.93)	1.81 ± 5.23	0.90	3
Ecdyonurus	−0.58 ± 1.19	0.38 ± 0.03	0.98	12	10.06 (7.67–13.20)	1.94 ± 0.21	0.97	13	10.79 (2.11–246.14)	2.13 ± 6.74	0.88	3
Hydropsyche	0.17 ± 0.90	0.36 ± 0.02	0.99	12	10.13 (7.56–13.58)	1.90 ± 0.23	0.97	13	10.87 (2.44–289.13)	2.11 ± 7.08	0.87	3
Gammarus	0.00 ± 0.78	0.31 ± 0.02	0.98	12	10.26 (8.79–11.99)	2.53 ± 0.14	0.99	10	9.03 (1.24–65.94)	2.59 ± 4.29	0.97	3
Baetis	−0.08 ± 1.01	0.31 ± 0.02	0.98	12	10.26 (8.86–11.85)	2.54 ± 0.13	0.99	10	8.81 (1.53–50.79)	2.64 ± 3.78	0.97	3
Potamophylax	−0.08 ± 0.82	0.19 ± 0.02	0.97	12	7.27 (4.34–12.19)	3.07 ± 0.66	0.98	5	6.80 (5.18–8.94)	3.23 ± 0.33	0.99	7

Table 4 Marking experiments: mean values for the percentage of animals dispersing, including (mean %D_1) and excluding (mean %D_2) lost animals, the ratio of number of animals moving upstream to those moving downstream (D_U/D_D), the median [Med. L (m)] and maximum [Max. L (m)] distances moved upstream and downstream (excluding animals assumed to have drifted downstream); 95% CL given for all values except Max. L (m)

	Mean %D_1	Mean %D_2	D_U/D_D	Med. L (m) up	Med. L (m) down	Max. L (m) up	Max. L (m) down
Perlodes	81.32 ± 1.77	90.28 ± 1.36	3.04 ± 0.15	4.06 ± 0.42	1.44 ± 0.07	13.5	3.0
Rhyacophila	71.83 ± 1.39	80.32 ± 0.89	2.76 ± 0.21	3.23 ± 0.60	1.08 ± 0.12	13.0	2.0
Isoperla	63.20 ± 1.29	70.59 ± 0.78	2.63 ± 0.19	1.98 ± 0.22	0.92 ± 0.10	9.5	1.5
Protonemura	46.39 ± 1.07	51.19 ± 0.61	2.00 ± 0.10	1.27 ± 0.14	0.98 ± 0.11	7.5	1.5
Rhithrogena	45.00 ± 1.43	50.22 ± 1.03	1.95 ± 0.20	1.29 ± 0.11	1.00 ± 0.10	8.0	1.5
Ecdyonurus	35.76 ± 1.02	40.07 ± 1.10	1.73 ± 0.25	1.08 ± 0.08	0.98 ± 0.11	6.5	1.5
Hydropsyche	36.11 ± 1.02	40.24 ± 1.43	1.72 ± 0.20	1.17 ± 0.14	1.00 ± 0.07	6.5	1.5
Gammarus	30.56 ± 0.65	34.13 ± 0.81	1.62 ± 0.23	1.00 ± 0.12	0.94 ± 0.10	6.0	1.5
Baetis	30.35 ± 1.45	34.04 ± 1.68	1.59 ± 0.19	1.04 ± 0.06	0.98 ± 0.11	5.5	1.5
Potamophylax	18.54 ± 0.99	19.68 ± 1.10	1.02 ± 0.30	0.85 ± 0.08	0.92 ± 0.08	3.5	3.5

were very similar to those obtained from the stream channels. Median dispersal distances were similar in the channel and marking experiments, but maximum upstream distances were higher for two species in the marking experiments, being 13.5 m for *Perlodes* (Fig. 6a) and 13 m for *Rhyacophila* (Table 4). Both species attained the maximum possible distance of 10 m in the channel experiments (Table 2). Apart from *Perlodes* and *Potamophylax* (Fig. 6b,h), maximum distances downstream rarely exceeded 2 m. The following exceptions probably drifted downstream: two *Isoperla* recaptured at downstream distances of 11.5 and 13 m, four *Gammarus* recaptured at 10 (two animals), 12.5 and 14 m downstream, and five *Baetis* at 11.5 (two animals), 13, 13.5 and 14 m downstream. These animals were not included in the estimates of median and maximum dispersal distances (Table 4).

In summary, the marking experiments produced results similar to those from the stream channels, thus increasing confidence in the estimated values, even though their precision was sometimes poor, especially when there were few data points (Tables 1 and 3).

Discussion

The inverse power function was an excellent dispersal model for all species, and its parameter estimates were similar within species in both the stream channel and marking experiments, but varied between species. The negative exponential and negative logarithmic equations both provided significant fits to some of the data sets in the present study, but their fit was

always poor compared with that of the inverse power function. Turchin (1998) criticised all these empirical models on the grounds that they lack a mechanistic basis, and suggested that models based on theoretical arguments, such as diffusion or random-walk models, are preferable. To apply such models to real data requires information that would be difficult to obtain for stream invertebrates. Tracking the paths of the dispersing animals is the ideal approach, but would rarely be feasible for stream invertebrates that often disperse whilst hidden within the stream bed. Mark-recapture is probably the most widely-used technique for studying invertebrate dispersal (Osborne, Loxdale & Woiwod, 2002). In the present study, it produced data that were similar to those obtained for unmarked animals in the stream channels and therefore the marking technique probably had no adverse effects on the animals in the stream.

Arguments continue over the role of density-dependent processes in the dispersal of stream invertebrates and evidence for and against is listed in the Introduction. Nearly all these studies dealt with only downstream dispersal, which is usually termed 'invertebrate drift'. The single study to examine both upstream and downstream dispersal simultaneously found that dispersal of *B. rhodani* was density-independent (Humphries, 2002). The number of larvae dispersing was proportional to benthic density, as in the present study, with the mean proportion of larvae dispersing being slightly lower at 28% than the mean values of 33 ± 1% in the stream channels and 34 ± 2% in the marking experiments. One possible reason for the absence of density-dependence for any of the 10
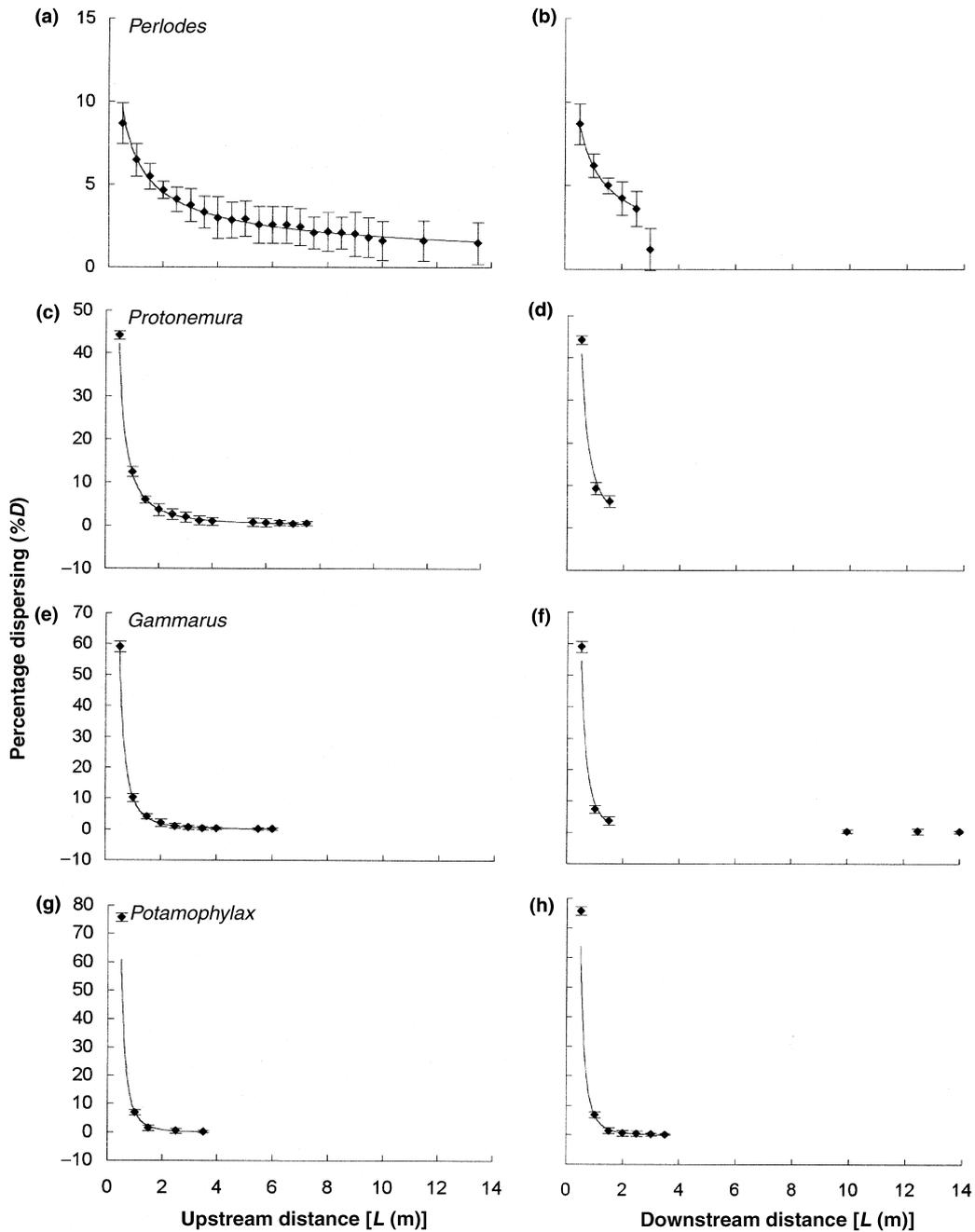
Fig. 6 Marking experiments: relationship between the distance travelled [L (m)] upstream (left panels) or downstream (right panels) and the proportion of animals travelling that distance (%D); curves given by equation 2 in Table 3. (a and b) *Perlodes microcephalus*, (c and d) *Protonemura meyeri*, (e and f) *Gammarus pulex* and (g and h) *Potamophylax cingulatus* (each point is the mean with 95% CL).

species in the present study was the use of animals greater than half-size. Density-dependent dispersal may be more important for smaller animals dispersing from egg clumps, and may be more frequent in laboratory experiments when densities are high, food

levels are low, water velocities are high, or the substratum type does not allow the animals to shelter in the interstices (Walton *et al.*, 1977; Walton, 1980).

An important finding of the present study is that dispersal was predominantly upstream for nine of the

10 species, the exception being the case-building caddis, *Potamophylax*. However, the strength of up-stream movement varied considerably between species, being strongest for the three carnivores, *Perlodes*, *Rhyacophila* and *Isoperla*, and weakest for *Gammarus* and *Baetis*. The dispersal ratios for the 10 species were strongly correlated with the proportion of animals dispersing. Therefore, the higher the proportion dispersing, the stronger was the upstream movement. These differences between species may partially explain the apparent contradictions of earlier work, with some studies concluding that upstream dispersal is negligible and others concluding that it is extensive (see references in Introduction). The extensive upstream movements of the present study may have been due to the use of animals greater than half-size, but an earlier study in the same stream showed that animals less than half-size moved upstream in large numbers, especially amongst small stones and gravel near the banks (Elliott, 1971a).

Several studies have recorded and modelled the distances travelled by downstream-dispersing invertebrates in the drift, and revealed large intraspecific and interspecific variation (references in Elliott, 2002a). There is a paucity of similar work on upstream dispersal, and no previous attempts to fit standard dispersal models. Prior to adult emergence, the North American mayfly, *Leptophlebia cupida* (Say) moved upstream at a rate of approximately 200 m per day in a Manitoba stream (Neave, 1930) and 10 m h^{-1} in an Alberta stream (Hayden & Clifford, 1974), and male *Gammarus fossarum* Koch moved upstream at a rate of up to 40 m h^{-1} (Meijering, 1972). These values are far higher than those obtained in the present study. However, some values are closer. Marked *G. pulex* moved 0.1–7.2 m upstream in 4 days (Rawer-Jost *et al.*, 1999), and self-marked case-building larvae of *Chyranda centralis* (Banks) moved upstream at up to 3.6 m per day, or remained near the release site, or moved downstream (Erman, 1986). Results for this latter species were similar to those obtained for the case-building larvae of *Potamophylax* in the present study. Upstream-downstream movements of *Potamophylax* also occurred in a Swedish stream but no information was provided on dispersal distances (Otto, 1971). The most detailed study of dispersal in a stream invertebrate is that of Freilich (1991) who tagged over 1000 larvae of the stonefly, *Pteronarcys californica*, in a Rocky Mountain stream. Most larvae

remained within a few metres of their first capture point, but a few moved up to 44 m downstream or 40 m upstream over a 3-month period, and some individuals moved rapidly upstream at a rate of 6–22 m per day. *Perlodes* was the only species in the present study that could approach these values, but its maximum upstream distance of 13.5 m per day was still well below the highest values for the North American species. From the limited information available for upstream dispersal distances, it can be concluded that values in the present study were not exceptional and were well within maximum values recorded for other species. Both the median and maximum dispersal distances upstream or downstream were correlated with the proportion of animals dispersing. Therefore, the higher the proportion dispersing, the greater the distance travelled. Seven of the species in the present study were included in an earlier experimental study on downstream drift (Elliott, 2002a) and their mean times spent drifting downstream (Table 2) correlated positively with the maximum dispersal distances ($r = 0.92$ with $n = 7$).

Unexpectedly, neither water velocity nor temperature had any significant effect on dispersal, especially as water velocity had a marked effect on downstream dispersal in the invertebrate drift (Elliott, 2002a). The range of mean water velocities in the 4 months of the experiments was quite large at 0.04–0.35 m s^{-1} in both the stream channels and the natural stream during the marking experiments. As the movements of the invertebrates on the stream bed occurred on or within the substratum (Elliott, 1971a), the dispersing animals were subjected to water velocities much lower than those in the water column above the stream bed. It is therefore possible that fluctuations in water velocity have little effect on dispersal, other than drift, or when velocities are exceptionally high during spates.

The 10 species of the present study can be arranged in decreasing order according to their dispersal abilities. The three carnivores (*Perlodes*, *Rhyacophila*, *Isoperla*) dispersed most rapidly (70–91% in 24 h) in both the stream channel and marking experiments, and travelled predominantly upstream ($D_U/D_D = 2.6$–3.1) with maximum distances per day of 9.5–13.5 m. Unfortunately, no information on drift times is available for these three species. *Perlodes* and *Rhyacophila* are both very active predators and their spatial distribution in the stream is very close to random in both the day and night, whilst *Isoperla* is

more aggregated at night when it is most active (Elliott, 2002d). Next came *Protonemura* and *Rhithrogena* in which about half the initial numbers (50–51%) dispersed, and travelled predominantly upstream ($D_U/D_D = 2$) with maximum daily distances of 7.5–8.0 m. The mean time spent in the drift was 33 s for both species, the same time as that for dead invertebrates, indicating no active settlement from the drift (Elliott, 2002a). Both species became more aggregated at night, except at low densities, indicating that their movement is chiefly nocturnal (Elliott, 2002d). Next in order were four species (*Ecdyonurus, Hydropsyche, Gammarus, Baetis*) in which less than half the initial numbers (33–40%) dispersed. They showed a weaker upstream preference ($D_U/D_D = 1.6–1.8$) and maximum daily distances of 5.5–7.0 m. All four species actively settled from the drift so that they spent only a short time drifting, especially *Gammarus* and *Baetis* (Table 2). It is notable that these mean times divide the four species into two sub-groups. Mean drift times were 17 and 22 s for *Ecdyonurus* and *Hydropsyche*, and 40% of both species dispersed in both the stream channel and marking experiments. Much lower mean drift times of only 9 s were recorded for *Gammarus* and *Baetis*, and only 33–34% of these species dispersed. Aggregation increased at night for *Ecdyonurus* and *Baetis*, indicating chiefly nocturnal movement, but did not change significantly from day to night for *Hydropsyche* (Elliott, 2002d). Few larvae (20%) of *Potamophylax* dispersed, with similar maximum upstream and downstream distances of 3.5 m in both the stream channel and marking experiments. Larvae of this species spent only 1–4 s in the drift and rarely drifted (Elliott, 2002a). In contrast to the other species, aggregation of *Potamophylax* larvae decreased at night when they were most active, and their nocturnal spatial distribution in the stream was very close to random. A similar day-night change in spatial distribution was shown by three other case-building caddis larvae, *Odontocerum albicorne* (Scopoli), *Sericostoma personatum* (Spence) and *Drusus annulatus* Stephens (Elliott, 2002d). These three species may therefore exhibit a dispersal pattern similar to that shown by *P. cingulatus* larvae.

Finally, the results of the present study can be considered as part of the broader topic of dispersal in freshwater invertebrates. The review by Bilton, Freeland & Okamura (2001) concludes that most dispersal is passive, often through transport by animal vectors or wind, and that active dispersal is relatively uncommon, apart from flight in adult freshwater insects. The present study shows that active dispersal of the aquatic stages is also common. Most work on dispersal by adult aquatic insects has been in relation to the 'colonisation cycle hypothesis': is there an upstream flight of ovipositing females to compensate for downstream drift? The short review by Petersen *et al.* (1999) provides little support for upstream flight in most species. However, a mark-recapture study using stable isotopes recorded a maximum upstream distance of 1 km for some adult *Baetis* in an Arctic river (Hershey *et al.*, 1993). Such dispersal may allow individuals to move from one headwater stream to another without lateral dispersal, larvae drifting downstream below the confluence of two streams and then adults flying upstream into either stream (Griffith, Barrows & Perry, 1998). A similar mechanism would also facilitate the dispersal of non-insects such as shrimps, and the present study has shown that upstream movements can be extensive for some species. Upstream dispersal and downstream drift means that there will be less isolation by distance within streams than between streams. A recent, and promising, development is the use of molecular markers to evaluate the frequency of dispersal in freshwater invertebrates. From their review of this work, Bilton *et al.* (2001) conclude that most genetic studies of stream insects demonstrate that populations in different stream systems show moderate to high levels of genetic differentiation, including evidence of cryptic speciation. They also conclude that dispersal rates within a drainage network appear to be higher than those between separate catchments, even in species capable of active flight. All this work indicates a wide variation in the dispersal abilities of different species of freshwater invertebrates. The species of the present study formed a continuum from rapid to very slow dispersers. These interspecific differences should be considered when evaluating the role of dispersal in the maintenance of genetic diversity in stream invertebrates, and in their ability to colonise or re-colonise habitats.

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